MORE VERTEBRATES, INCLUDING A NEW MICROSAUR, FROM THE UPPER PENNSYLVANIAN OF CENTRAL COLORADO

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ABSTRACT: More fossils, mostly vertebrate, have been collected from a black shale low in the Sangre de Cristo Formation in the Arkansas River valley of central Colorado. Some of the fossils probably represent "residents" in the pond, but most of the bones seem to have been washed in from nearby. None of the recently found specimens conflicts with the estimate of Late Pennsylvanian, probably Missourian, age based on the previously reported fossils (Vaughn, 1969); and recognition of the pelycosaur *Edaphosaurus* cf. *E. ecordi* corroborates this estimate. The presence of bisaccate gymnosperm pollen is attributed to proximity of the area to elements of the Ancestral Rocky Mountains. An almost complete, articulated skeleton of a new kind of microsaur requires the naming of a new genus and species, *Trihecaton howardinus*. This form is clearly a microsaur, as shown by the structure of the first vertebra and the character of the scales; but it is remarkable in the infolding of the enamel of the marginal teeth, and in the possession of large presacral intercentra with capitular facets. There are also large intercentral haemal arches. A new family, Trihecatontidae, is based on the genus, but the position of this family within the Microsauria is obscure. *T. howardinus* seems primitive in a number of respects, but it occurs too high in the stratigraphic column to be regarded as an actual "urmicrosaur." More materials of the diadectid *Desmatodon hesperis* are now on hand. A braincase and connected parts of the dermal roof of an apparently immature specimen show essential similarity to the Early Permian *Diadectes*, but the basipterygoid joint was mobile, and, as rarely seen in *Diadectes*, there are narrow fenestrae between the postparietal and tabular regions. The teeth of a juvenile maxilla contrast with those of the holotypic maxilla in several ways: smaller number, much greater relative length and more incisiform aspect of the first two, separation by longer spaces, and lack of wear facets. An analysis of the replacement cycle of the teeth in the holotypic maxilla of *Desmatodon hesperis* shows a much longer replacement wave than in *Diadectes*, and also reveals the existence of a "gap" between the second and third teeth. In its longer replacement wave, *Desmatodon hesperis* may also differ from the type species, *Desmatodon hollandi*, and it may become necessary to set up a new genus. The problems of the origin and affinities of the diadectids remain unsolved.

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INTRODUCTION

I have recently published on vertebrate fossils found low in the Sangre de Cristo Formation of central Colorado (Vaughn, 1969). These fossils, which seem to be of Late Pennsylvanian, more specifically Missourian, age represent the only sizable North American tetrapod fauna of that age known from west of the Garnett quarry of eastern Kansas (see Peabody, 1952), although tetrapod trackways are known from elsewhere in the Pennsylvanian of Colorado. They are of special interest in that they occur in the region of the Ancestral Rocky Mountains of late Paleozoic time. The present paper is a report on additional materials recently recovered from the same site; these include remains of new faunal elements, an almost complete skeleton of a new kind of microsaur, and materials that contribute significantly to our understanding of the only known Pennsylvanian diadectid, *Desmatodon.*

The quarry is near the town of Howard in the valley of the Arkansas River, in NW¼ NE¼ SW¼ sec. 22, T 49 N, R 10 E, Fremont County, Colorado. It is about 1450 feet above the base of the Sangre de Cristo Formation as defined by Brill (1952) in a two- to three-foot thick black shale that he designated as part of "Interval 300"; the total thickness of the formation in this region is about 8800 feet. The steeply dipping attitude of the beds has made quarrying difficult, and the shale is not yet completely exposed, but it may be said in general that it is a lens-shaped deposit that probably represents a pond, perhaps an oxbow within the general system of stream channels indicated in this part of the formation. The presently exposed face is about 70 feet in length, from where it is cut by a small stream that flows close to a soil-covered bank, to where it pinches out to the northwest. A study of the layering of the shale and the pattern of distribution of the fossils within the shale is in progress and will be reported at a later date.

I have been fortunate to have had access to Mr. Walter Pierce's manuscript on the stratigraphy of the Howard area (unpublished master's thesis, Colorado School of Mines, 1969), which has assisted greatly in my field work. The Interval 300 quarry is in the upper part of Pierce's "Unit V"; within the lower part of this unit, which has a maximum thickness of about 3700 feet, lies the limestone that Brill (1952) correlated with the Whiskey Creek Pass Limestone to the south and with the Jacque Mountain Limestone to the north. The Sangre de Cristo Formation as defined by Brill begins directly above this limestone. Pierce demonstrates an angular unconformity between Unit V and the overlying Unit VI, but it is not yet known how much time is represented in this break. Pierce also shows that the dominant sedimentary pattern of Unit V is the point-bar type, with streams that flowed generally toward the northwest.

The Sangre de Cristo Formation was deposited in the southern half of the trough that lay between the Late Pennsylvanian and Early Permian Front Range to the east and the Uncompahgre Highland to the west. Mallory (1958, 1960) has presented paleogeographic reconstructions of the trough and surrounding highlands. There is some debate as to the proper name of the formation; Brill (1952) extended the name Sangre de Cristo northward from New Mexico and southern Colorado, but Chronic (1958) has recommended that this name not be used in central Colorado and that instead the older term, Maroon, be retained to emphasize the essential continuity of the beds with the Maroon Formation deposited in the northern half of the trough. Geologists at the Colorado School of Mines are currently engaged in studies of the general region around the Interval 300 quarry, and more detailed stratigraphic analyses will soon appear, but for the present we may rely on Brill's terminology. It must also be noted that the lower parts of the Sangre de Cristo Formation, in Brill's usage of the term, are not everywhere of the same age; in central Colorado the lower part, which includes Interval 300, is apparently Late Pennsylvanian, but the equivalent strata in northern New Mexico are marine and are assigned to the Madera Formation whereas the terrestrial Sangre de Cristo Formation as mapped there is probably entirely of Early Permian age (see Brill, 1952; Vaughn, 1969).

ADDITIONS TO THE FLORA AND FAUNA

Most plant remains from the Interval 300 quarry are very poorly preserved, but there are carbonized bits of wood, and *Calamites* impressions are recognizable. Stratigraphically somewhat lower, but still within Pierce's Unit V and above the limestone correlated with the Whiskey Creek Pass Limestone by Brill, better preserved plants are found in SW¼ SW¼ NW¼ sec. 22. These include *Calamites* pith casts, carbonized impressions of *Walchia* fronds, and impressions of fernlike plants. Below this, in Pierce's Unit IV—roughly equivalent to the upper part of the Minturn Formation of Brill's usage—are found more *Calamites* remains and also bisaccate gymnosperm pollen, which latter Scott (1967) takes as an indication of Permian rather than Pennsylvanian age. Microscopic examination of the black shale of Interval 300 also reveals bisaccate gymnosperm pollen. This may seem to conflict with the evidence presented earlier (Vaughn, 1969) and below for Late Pennsylvanian age of Interval 300, but not necessarily. Clapham (1970), in a study of Permian pollen from Oklahoma, came to the conclusion that gymnosperms producing bisaccate pollen were upland forms. Langenheim (1959:569) has pointed out that our picture of late Paleozoic plant successions is based largely on the record from farther east, where extensive uplands did not exist in the Pennsylvanian, and that, therefore, "lowland plants became known as Pennsylvanian indices and upland plants as Permian indices in the mid-western and eastern United States. . . however, the upland environments of the Ancestral Rockies were close to the marginal swamp and marine environments early in the Pennsylvanian. The result is the presence of 'Permian' plants in intimate association with 'Pennsylvanian' plants and marine invertebrates." Elias (1970:696) accounts in much the same way for recent discoveries of *Walchia*, previously not known to occur below the Upper Pennsylvanian, in the Middle Pennsylvanian of Oklahoma; he feels that "*Walchia* undoubtedly existed . . . in the ancient highlands which rose in conjunction with the very early Pennslyvanian orogenies in the areas of the Arbuckle and Ouachita uplifts." The principle is similar to that expressed by Axelrod (1952) when he suggested that angiosperms may have been present in the Permian and Triassic, but "hidden" in uplands remote from the lowland areas of deposition. It seems probable that the presence of bisaccate gymnosperm pollen in and even below Interval 300 is only a matter of ecological difference, that is, a reflection of the upland conditions of the nearby Ancestral Rocky Mountains and not really inconsistent with the more compelling evidence of Late Pennsylvanian age presented by the vertebrates.

Shells of small pelecypods were noted in my earlier paper; the only other invertebrate remains that have been recognized in Interval 300 are parts of carapaces of the branchiopod *Cyzicus*.

The vertebrates known to date from Interval 300 are:

- Elasmobranch fishes
    - A xenacanth
- Palaeoniscoid fishes
    - One or more kinds
- Labyrinthodont amphibians
    - ?Anthracosaurs
        - A large ?embolomere
    - Temnospondyls
        - Several small rhachitomes including the dissorophid ?*Amphibamus*
- Lepospondyl amphibians
    - Aistopods
        - *Coloraderpeton brilli* Vaughn, 1969
    - Microsaurs
        - *Trihecaton howardinus*, new genus and species
- ?Cotylosaurs
    - *Desmatodon hesperis* Vaughn, 1969
- Pelycosaurian reptiles
    - A "medium-sized" ophiacodont
    - A small sphenacodont
    - *Edaphosaurus* aff. *E. raymondi* (Case, 1908)
    - *Edaphosaurus* cf. *E. ecordi* Peabody, 1957

The additions to my earlier list are: the xenacanth, the dissorophid labyrinthodont, the new microsaur, and *Edaphosaurus* cf. *E. ecordi*; it is also now clear that I am dealing with more kinds of small rhachitomes than I previously recognized. The great difficulty is in the disarticulated nature of almost all the materials, which occur mostly as isolated bones. It is obvious that more faunal elements are represented than can be identified.

The xenacanth "shark" is represented by only one spine (UCLA VP

1736[1]), but this, with its two rows of recurved denticles, is sufficient for identification. The presence of this freshwater form at this site is no surprise.

The remains of palaeoniscoid fishes are frustrating. Mostly, the scales are isolated, but they also occur in articulated patches, and sometimes small parts of skulls and fins are found in association with these patches. The scales are almost all small, smooth and shiny, with diamond-shaped outlines and with the peg-and-socket articulation common among palaeoniscoids, but rare signs of different scales indicate the presence of more than one kind of palaeoniscoid. That these thin scales are found in patches as often as they are would seem to indicate that palaeoniscoids, at least, were "resident" in the pond. Perhaps also to be counted as a resident is the aistopod, *Coloraderpeton brilli*, vertebrae and osteoderms of which are frequently found in articulation or very close association. It may even be that trails of tiny pellets found in a number of places in the quarry are the result of burrowing activity of this aistopod. The presence of coprolites, some containing palaeoniscoid scales, also points to a resident fauna. The scattered remains of almost all the other faunal elements seem to indicate that they were washed in from elsewhere, but parts of what was apparently a single individual of *Desmatodon hesperis* were found not far removed from one another on the same plane, and the specimen of the microsaur described below is almost complete and in nearly perfect articulation. There are no signs of wear on the bones that would indicate transportation from a distant source. It is possible, of course, that some of the scattering of the bones may be due to predatory activity of the xenacanths, but the lack of any discernible bite marks makes it seem more likely that the specimens were washed in from the immediately surrounding area, perhaps during periods of flooding of the adjacent streams.

In my earlier paper, I illustrated premaxillary and palatine bones (UCLA VP 1700 and 1699) of what I took to be a large rhachitomous labyrinthodont. More cranial parts of this form (UCLA VP 1737) are now at hand, including another premaxilla and an associated large part of a dentary bone with small teeth that are slightly recurved at their tips. The premaxilla has a formidable tusk of about 25 mm length, with an oval base 10 mm long but only 6 mm wide. All the teeth show deep infolding of the enamel and dentine in their basal portions. The general shape of the preserved part of the dentary and the traces of the meckelian fenestrae cause me to think that, contrary to my earlier identification, this form may be an anthracosaur, perhaps an embolomere similar to the large *Neopteroplax conemaughensis* described by Romer (1963) from the Conemaugh Group of Ohio. Other elements, including a squamosal bone (UCLA VP 1701), seem to support this. Better materials must be found before a positive identification can be made, but it is clear that a labyrinthodont amphibian of crocodilelike proportions was present in the area.

[1] The designation UCLA VP refers to the vertebrate paleontological collection of the University of California, Los Angeles.

Many parts of small to "medium-sized" rhachitomes are represented in the collection from Interval 300. Some of these, as a fairly well-preserved dentary bone with slim, conical teeth (UCLA VP 1738), are of trimerorhachoid aspect; but most are indeterminate. One small, slender dentary with numerous, tiny teeth (UCLA VP 1739) seems clearly to be of a dissorophid. It falls within the size range of dentaries of *Amphibamus lyelli* from the uppermost part of the Allegheny Group of Ohio (Carroll, 1964), which it closely resembles, and it may represent a species of that genus.

Descriptions of remains of a number of pelycosaurian reptiles including a "medium-sized" ophiacodont and a small sphenacodont were given in my earlier paper. More materials of these forms continue to appear. These include: the basi-parasphenoid part of a braincase of the ophiacodont (UCLA VP 1740), with a distance of 26 mm between the lateralmost points of the basipterygoid processes; and a vertebra of the small sphenacodont (UCLA VP 1741), with a centrum about 11 mm long and a neural arch that shows the characteristic excavations on its lateral surfaces. These finds help to demonstrate the taxonomic diversity of the fauna and also reinforce the developing picture of a variety of pelycosaurs in the Late Pennsylvanian (see DeMar, 1970).

My earlier paper also recorded the presence of the little edaphosaurian pelycosaur *Edaphosaurus* aff. *E. raymondi.* It is now evident that there was also another small edaphosaur. UCLA VP 1742 is a partial neural spine that is strikingly similar in both shape and size to the spine of *Edaphosaurus ecordi* Peabody, 1957. As in that species, the spine is laterally flattened but flares distally within the anteroposterior plane and has only incipiently developed tubercles along the sides. The holotype of *E. ecordi* was found near Garnett in eastern Kansas, in a shale that forms part of a lagoonal deposit within the Stanton Formation, Missourian Stage, Upper Pennsylvanian (see Peabody, 1952). The general nature and fauna of the Garnett quarry, from which come the only known specimens of the reptile *Petrolacosaurus kansensis*, are quite different from the Interval 300 quarry, but Peabody (1957:949) points out that the holotype of *E. ecordi* was found near the bottom of the lagoonal deposit, "in heavily carbonaceous shale containing a more typical, coalswamp flora than higher and off-shore deposits in the lagoon."

The new specimens of *Desmatodon hesperis* and the holotype of the new microsaur are described in detailed fashion below. There remain, of course, many skeletal elements that defy taxonomic identification at this time, but they do indicate the presence of a diverse fauna and hold out the promise of further interesting finds.

I have already shown that the vertebrates previously reported indicate Late Pennsylvanian, probably Missourian, age (Vaughn, 1969). This is based largely on the essential similarity of *Desmatodon hesperis* to *D. hollandi* known from the middle part of the Conemaugh Group west of Pittsburgh, Pennsylvania. The association of remains of *Edaphosaurus raymondi* with the holotype of *D. hollandi* supports this estimate of approximate time-equivalence. The primitive nature of the aistopod from Interval 300, *Coloraderpeton brilli*, may perhaps also be cited as evidence for Pennsylvanian, rather than Permian, age.

There is nothing among the recently found vertebrate materials from Interval 300 that would contradict Missourian age; rather, *Edaphosaurus* cf. *E. ecordi* provides corroboration. Sturgeon and Hoare (1968) place the Stanton Formation, from which comes the holotype of *E. ecordi*, at about the same level as the Ames Limestone of the Conemaugh Group. The Round Knob Formation, from which comes the holotype of *Desmatodon hollandi*, lies shortly below the Ames. The Stanton Formation is near the top of the Missourian Stage and thus a closer, but not necessarily more accurate, estimate of the age of Interval 300 might be late Missourian. Nor does an estimate of Missourian age conflict with any other data—excepting perhaps the bisaccate gymnosperm pollen which, as I have said, may merely reflect environmental difference; according to Brill (1952), the Sangre de Cristo Formation in the area of Interval 300 rests conformably on rocks of Desmoinesian (Middle Pennsylvanian) age.

A NEW MICROSAUR

A well-preserved, articulated skeleton of a hitherto unknown kind of microsaurian amphibian is remarkable in a number of features that make it important in consideration of the origin and relationships of the Microsauria. Its distinctness from all previously known microsaurs requires the naming of a new family.

Order MICROSAURIA Dawson, 1863

TRIHECATONTIDAE, new family

This family is based on the new genus *Trihecaton*, described below. Because this is the only known genus, definition of the family is tentative: microsaurs with infolded enamel on the marginal teeth, and with large presacral intercentra with capitular facets for the ribs.

Trihecaton, new genus

Type species: ***Trihecaton howardinus***, new species.

Diagnosis: Marginal teeth simple cones with shallow infolding of enamel. Prominent coronoid process on lower jaw. Thirty-six presacral vertebrae—as nearly as can be determined. First vertebra of characteristic microsaurian structure, with forward-facing articular facet on either side of short "odontoid" process on anterior face of centrum, and deep notochordal pit on posterior face; two costal facets on either side of first centrum; first neural arch incomplete dorsally. Pleurocentra the dominant central elements, but large intercentra, with capitular facets, in presacral vertebral column. Intercentral haemal arches in tail. Almost regular alternation in shape of presacral neural spines. Presacral ribs articulate with transverse processes low on anterior parts of neural arches and also with intercentra. Stem of interclavicle very short, with abrupt termination. Well-developed limbs. Entepicondylar foramen in humerus. Scales of characteristic microsaurian pattern, with radiate striae.

Etymology: Named for the Interval 300 quarry. From the Greek *treis*, three, and *hekaton*, hundred.

Trihecaton howardinus, new species

Holotype: UCLA VP 1743 (Figs. 1; 2; 3, A-C), an articulated skeleton that lacks most of the skull although a maxilla and a mandible are present. The entire presacral vertebral column and most of the ribs are preserved. There are large parts of the left pectoral girdle and the interclavicle, and most of the left front limb, as well as parts of the right front limb. The pelvic girdle is poorly preserved, but the left femur is complete, and the distal half of the right femur is also preserved. Scales are present throughout the region of the vertebral column.

Referred specimen: UCLA VP 1744 (Fig. 3, D), a partially articulated series of twelve caudal vertebrae with haemal arches. Same kind of scales present as in holotype. Found immediately adjacent to the plastered-out block of matrix that contained the holotype, and probably part of the same individual.

Horizon and locality: Collected by a field party from the University of California, Los Angeles, in the summer of 1970, from Interval 300 of the section of the Sangre de Cristo Formation measured by Brill (1952:870), about 1450 feet above the base of the formation, in NW¼ NE¼ SW¼ sec. 22, T 49 N, R 10 E, Fremont County, Colorado. The age is Late Pennsylvanian, probably Missourian. In European terms, the horizon would be within the lower part of the Stephanian Series. The species is named after the nearby town of Howard.

Diagnosis: The same as for the genus as this is the only known species, but a note on size may be appropriate. The length of the skull, as known from the lower jaw, is about 2.5 cm, and the length of the presacral vertebral column is about 16 cm.

Description: Most of the features of the holotype and the referred specimen can be readily seen in the illustrations (Figs. 1, 2, 3). The anterior quarter of the presacral vertebral column is bent to the right and backward. The girdles and limbs are in their proper places relative to the column, but the maxilla, mandible and the few other preserved cranial fragments are displaced and lie adjacent to the interclavicle.

The left maxilla lies directly behind the interclavicle. It seems to be nearly

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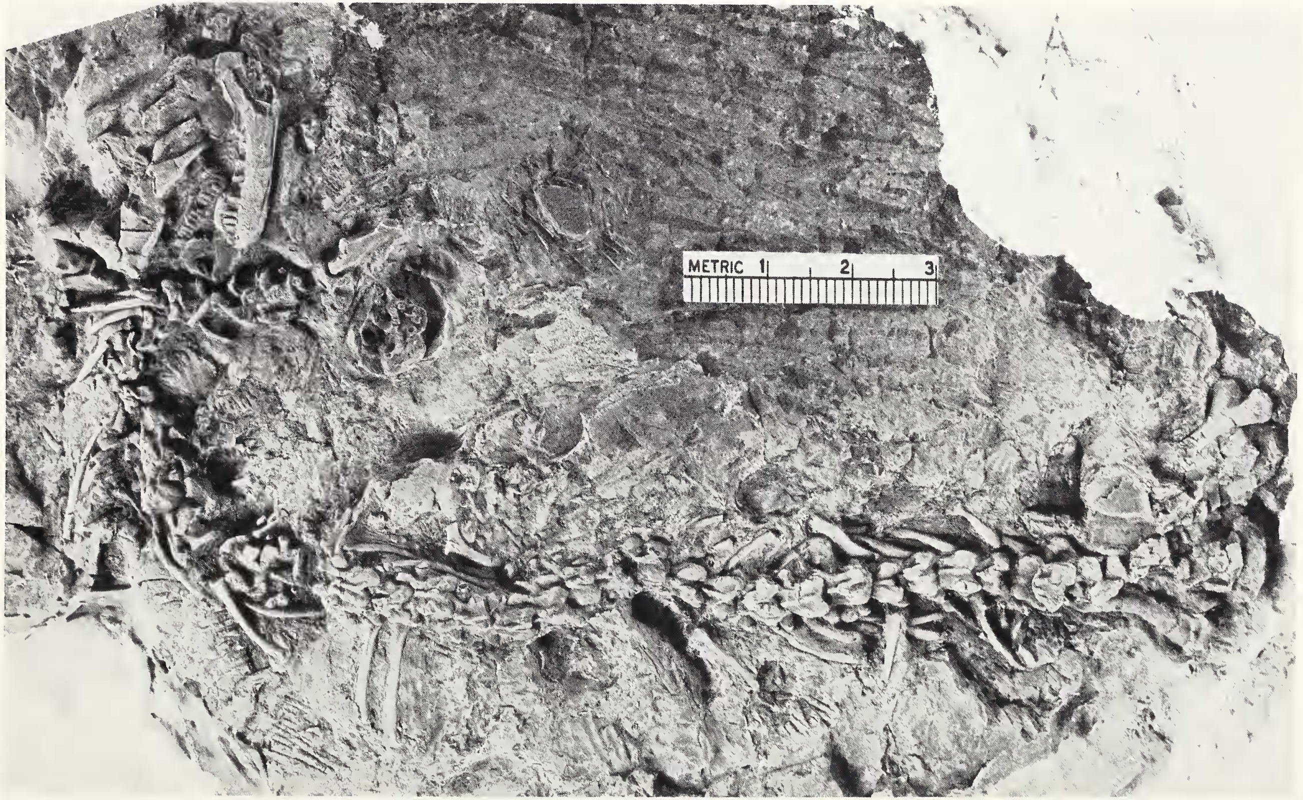
FIGURE 1. *Trihecaton howardinus*, new genus and species: photograph of the holotypic specimen, UCLA VP 1743. Dusted with white powder to bring out details. White material surrounding the matrix is plaster. Smallest divisions on the scale are millimeters.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complete except for the lack of a small posteriormost part. As preserved, it is 14 mm long; its greatest depth, about 2 mm, occurs about a third way back in its length, and posterior to this it tapers gradually to a depth of less than 0.5 mm. Nineteen slender, conical teeth are present, and there are spaces for three more. The anteriormost two are very slightly recurved, but the rest are straight. The longest, about 1.8 mm, are in the region of greatest depth of the maxilla; anterior to this they become slightly shorter, and posteriorly they

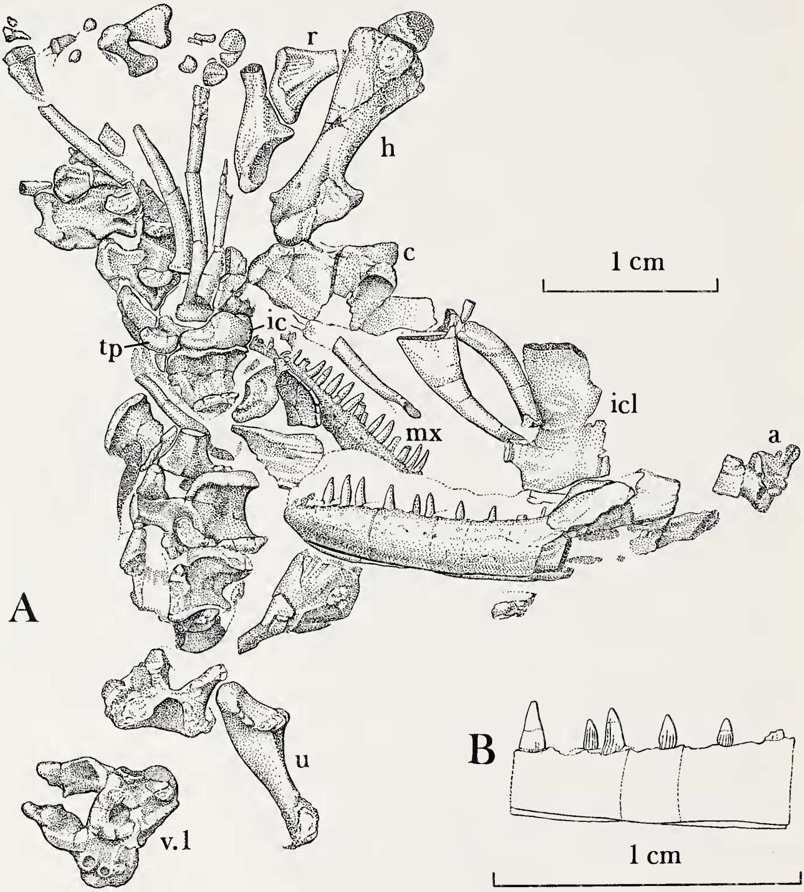

FIGURE 2. *Trihecaton howardinus*, new genus and species: details of holotypic specimen, UCLA VP 1743. A, anterior part of holotype, with mandible in lateral view, elements of pectoral girdle in internal view, and vertebrae in various views—first vertebra seen from behind; B, mandibular teeth at greater magnification. Abbreviations: a, articular region of mandible; c, coracoid plate; h, left humerus; ic, intercentrum following vertebra 6; icl, interclavicle; mx, maxilla; r, left radius; tp, transverse process of vertebra 7; u, right ulna; v. 1, first vertebra. Size indicated by the 1 cm scales.

decrease gradually to very small size—the exact length of the posteriormost teeth cannot be determined, due to breakage. A number of the teeth clearly show infolding of the enamel, expressed externally by fine grooves that are especially obvious in the basal portions; that the infolding is shallow is evident from the fact that those teeth that were worn, either prior to or during preparation, lack the grooves.

Almost all of the left mandible is preserved, exposed in lateral view. Although the posterior portion of the surangular, to which is attached an articular bone that projects mediad as a long spur, is broken and slightly displaced from the rest of this element, the clean fracture premits confident measurement of the total length of the mandible, 26 mm; this provides, of course, an excellent index to length of skull. The lateral surface of the mandible, especially the dentary, is irregularly pockmarked by small, subcircular pits; this is also true of the maxilla. The mandible is slender in most of its length, with a depth of only 3 mm midway along the tooth row, but posteriorly it rises in a prominent coronoid process, 6 mm deep, in which region the dentary overlaps the anterior part of the surangular and is capped by a conspicuous coronoid bone. The dentary meets a long splenial along the ventral border of the mandible. The angular bone is badly fractured, but it seems to have extended about as far posteriorly as did the surangular. Nine teeth are preserved in their entirety, stumps of three others are present, and there are spaces for about seven more. As in the maxilla, the teeth are slender cones, with the more anterior ones slightly recurved. Five of the teeth clearly show the grooves related to the infolding of the enamel; these grooves are more

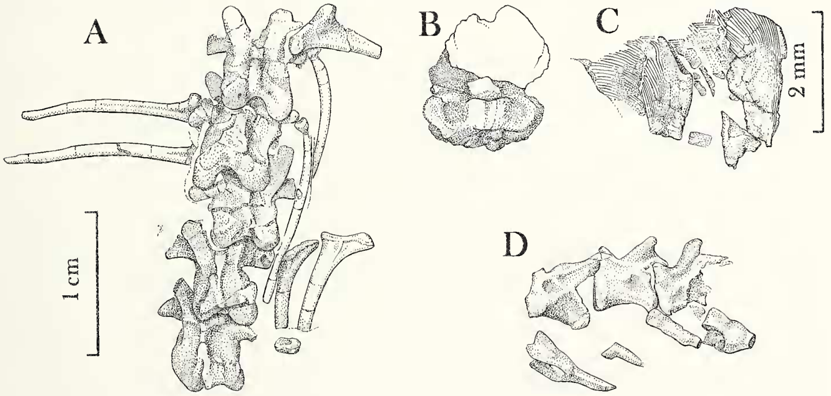

FIGURE 3. *Trihecaton howardinus*, new genus and species: details of holotypic specimen, UCLA VP 1743, and referred specimen, UCLA VP 1744. A, vertebrae 17-21 of holotype in dorsal view, and associated ribs; B, first vertebra of holotype in anterior view, some matrix left adherent to permit reunion with rest of specimen; C, fragmentary scales taken from near vertebra 17 of holotype; D, caudals from posterior portion of vertebral string of referred specimen. Size of A, B and D indicated by the 1 cm scale; size of C indicated by the 2 mm scale.

prominent at the bases but extend about three-quarters of the way up the teeth. In the rest of the teeth, which are worn, the grooves are not apparent. As in the maxilla, the longest teeth, about 1.8 mm, lie a short distance back in the jaw; anteriorly and posteriorly the teeth become shorter, with the shortest lying just in front of the root of the coronoid process. The anteriormost teeth are preserved only as stumps, and their exact lengths cannot be ascertained.

A few scraps of other cranial elements lie near the maxilla and mandible, but they cannot be identified with confidence.

As nearly as can be determined, there are 36 presacral vertebrae, in a column that was about 16 cm long. What I count as the last presacral has been pushed upward to partially override the poorly preserved, but obviously more massive, remains of what I judge to be a sacral, closely appressed to the pelvic girdle. The first vertebra is displaced from the second by several millimeters, but there is no evidence of an intervening vertebra. It is conceivable that there may have been 37 presacrals, but I am fairly confident that 36 is the correct number. There seems to have been only one sacral, but this cannot be stated positively. Scraps of caudals are present in the holotype, but the nature of the caudals is evident only in the referred specimen, and their number is unknown. Slight rotation and displacement of various vertebrae in the anterior part of the column display some in lateral, some in ventral, and some in dorsal view. Farther posteriorly, most of the vertebrae are seen in dorsal view, but rotation of vertebra 14 and loss of the neural arches of 15 and 16 allow intercentra to be seen in that region—as well as in the anteriormost parts of the column. These circumstances are fortunate, because the highly fissured nature of the matrix would make it hazardous to attempt to display the column from below.

Wherever in the column a series of well-preserved vertebrae is exposed in dorsal view, there can be seen an almost regular alternation in the shape of the neural spines. This is especially clear in vertebrae 17-21 and 26-35. The alternation is not quite as marked as in *Pantylus* (Carroll, 1968) but is pronounced nevertheless. In the "low" type (e.g., vertebrae 27 and 29), the spine runs the entire length of the neural arch as a low, rounded ridge. In the "high" type (e.g., vertebrae 28 and 30), the low ridge occupies only the anterior half of the arch; posteriorly, the spine broadens abruptly, rises slightly higher, and sends a short process forward. In the more anterior portions of the column this process is generally single, but posteriorly it is divided into a side-by-side pair of processes. That the alternation is not completely regular is shown by vertebrae 17-21, where the sequence is low-high-low-high-high. The significance of this alternation, which occurs also in other late Paleozoic tetrapods, is obscure. I have attempted an analysis of a similar pattern in the Early Permian reptile *Captorhinus* in terms of the system of interspinous ligaments, with particular regard to an "extended nuchal ligament" (Vaughn, 1970), but the presence of this pattern in the long-trunked *Trihecaton* casts doubt on such an explanation.

The first vertebra fits so well into the general microsaurian pattern (see Carroll and Baird, 1968) that only its salient features need description. Its length, from the tip of the "odontoid" process to the posterior edge of the centrum, is 4 mm. The "odontoid" process, on the anterior face of the centrum, is short, is rounded on its anteroventral surface, and is channeled by the neural canal on its dorsal surface. On either side of this process is a large, subcircular, slightly concave articular facet for the occiput; these facets face directly anteriad. The distance between the tips of the winglike buttresses for these facets is 7.5 mm. Each of these wings has on its posterolateral surface two small, slightly raised and centrally dimpled facets, one above the other; these are obviously for the first rib. The posterior face of the centrum, with a deep notochordal pit, has a width of only 3.5 mm. The greatest height of the centrum is 4 mm; the highest points of the neural arch are 8 mm above the bottom of the centrum. The lateral halves of the neural arch almost meet at a point anteriorly, but posteriorly they diverge widely. A short, blunt spine rises above each posterior zygapophysis. The lack of junction of the halves of the neural arch is not unique; Miss Eleanor Daly (personal communication, 1971) has shown me a similar condition in certain microsaurs from the Lower Permian of Oklahoma.

The shape of the centra (pleurocentra) can be easily made out in several of the anterior vertebrae and also in the region of vertebrae 14-16. In general, the centra are like those of the microsaur *Tuditanus* (see Peabody, 1959; Carroll and Baird, 1968). They are notochordal, are excavated on their lateral surfaces in such a way that they appear pinched, and a rounded ridge forms the concave ventral border. They are different from those of *Tuditanus* in that the ventral portions of both the anterior and posterior lips of the centra are bevelled for the reception of the large intercentra. The centra that can be measured are each somewhat more than 4 mm long, and are about 5 mm wide and 3.5 mm high at the posterior end. Vertebrae 15 and 16 show that the floor of the neural canal paralleled the hourglass-shaped notochordal canal.

The neural arches are not swollen. They are firmly joined to the centra, but the lines of the neurocentral sutures are evident as curved ridges. The neural spines have already been described. The zygapophyses are oval with long anteroposterior axes, with their articular surfaces in the horizontal plane. Stout transverse processes about 1.5 mm long occur near the junctions of the neural arches and centra on all the presacral vertebrae excepting the first, and possibly the second, which is poorly preserved. They are kidney-shaped in cross-section, concave side to the rear, with the upper end lying approximately midway in the length of the vertebra and the lower end near the front edge of the centrum, apparently in contact with the apex of the intercentrum. The costal facets of the transverse processes face forward, laterally and ventrally.

An intercentral scrap is visible in front of the second vertebra, large parts of the intercentra are exposed in front of vertebrae 3 and 6, and a complete one lies in apparently its life position against the posterior rim of the centrum of vertebra 6. Parts of intercentra may also be seen in front of vertebrae 14, 15 and 17. The intercentrum in front of vertebra 14 seems to have been as large as the one behind vertebra 6; this, plus the presence of large haemal arches in the caudal series, makes it seem likely that intercentra were present throughout the entire presacral column.

As shown by the one behind vertebra 6, the intercentrum is a large crescent that extends halfway up along the bevelled lip of the centrum. The ventral portion is much swollen toward the sides, almost bulbous, and has an anteroposterior length of 2 mm, almost half as long as the centrum. On either side, the wedge-shaped ascending part of the intercentrum bears a large, concave articular facet that faces posteriorly as much as it does laterally. This ascending part is abruptly truncated where it meets—actually lies against—the ventral end of the transverse process. This proximity of capitular and tubercular facets is consonant with the structure of the ribs described below. The intercentrum in front of vertebra 14 also shows the capitular facet.

The first several ribs are not preserved, but the costal facets on the first vertebra show that ribs must have been present in this region. Indeed, the well-developed transverse processes back to and on the last presacral, plus ribs either articulated or in close association with almost all the vertebrae, show that there were ribs throughout the presacral column. The ribs articulated on the left sides of vertebrae 18 and 19 have gradually tapered shafts about 14 mm long. Ribs farther forward in the column have expanded distal ends. The structure of the head is best seen in partial ribs lying to the right of vertebrae 17 and 19. The dorsoventral length of the head is about 4 mm. The strongly convex capitulum is separated by only 0.5 mm from the slightly concave tuberculum; the connecting web is much thinner than either the capitulum or tuberculum, but its margin is not incised. Distal to the head the shaft narrows rapidly. Wherever else the heads of ribs can be seen, including the anterior part of the column, the pattern is similar, and what can be seen of the ribs immediately anterior to the pelvic girdle indicates that articulation was with both transverse process and intercentrum throughout the presacral column, excepting of course the first rib.

The referred specimen contains parts of twelve caudal vertebrae. Two of these, in articulation but displaced from the rest, have transverse processes that are fairly well developed but without the ventrad prolongations seen in the presacral vertebrae. Intercentral elements are not attached to these two vertebrae, but the bilaterally bevelled surfaces of the posteroventral parts of the centra indicate that haemal arches were present. The other ten vertebrae, of which the most anterior is represented by only a fragmentary haemal arch, are in one string, but two vertebrae midway in this string have undergone rotation in the vertical plane. This displacement of parts is in accord with the jumbled nature of the pelvic bones of the holotype. A vertebra toward the anterior end of the string has a small transverse process, but only small nubbins are present in the same positions on the more posterior vertebrae. The neural spines are thin, short, and inclined somewhat posteriad; there is no sign of alternation in shape. Posteroventrally directed haemal arches are present throughout the string; they are clearly separate from the centra, between which their proximal ends are wedged. A well-preserved haemal arch toward the posterior end of the string is 7 mm long. Part way along the length of each haemal arch, coinciding with the ventral limit of the haemal canal, there is a bulbous swelling; distal to this the arch tapers, ending in a slight dilatation in the more anterior ones, in a point in the more posterior ones. The swollen portion comes to lie more proximally farther back in the string. A bridge of bone completes the haemal canal dorsally. As previously mentioned, the referred specimen also includes scales identical to those of the holotype. There is also a metatarsal or phalangeal element.

Although the pectoral girdle of the holotype is not entirely preserved, it is clear that in most features it resembles that of *Pantylus* (see Carroll, 1968). A fragmentary element on the left side of the interclavicle may be part of a cleithrum or clavicle, but this is not certain; an adjacent element seems to be a displaced anterior rib with expanded distal end. The interclavicle is seen in internal view. It is T-shaped, with an expanded bowl that must have been about 15 mm in width but, quite unlike *Pantylus*, the stem is very narrow and remarkably short, only about 1 mm. This shortness does not appear to be due to fracture; at its termination the stem dilates slightly and ends abruptly in a rugose surface. It would almost seem that it was continued in cartilage, but this is highly unlikely in a dermal element. The coracoid plate of the left scapulocoracoid, which lies in the region of vertebrae 4-6, is exposed in internal view. Most of the scapular blade is missing, but it is clear that, as in *Pantylus*, it joined the coracoid plate anterior to the glenoid fossa. Also as in *Pantylus*, the glenoid fossa is buttressed anteriorly by a ventrad projection along which the articular surface is continued, and the part of the coracoid plate posterior to the fossa is short and narrow. There is a coracoid foramen medial to the junction of the scapular blade and coracoid plate. The greatest anteroposterior length of the scapulocoracoid seems to have been about 13 mm.

Only the proximal portion of the right humerus is preserved, but the left is complete and is nearly in articulation with the glenoid fossa. As in both *Tuditanus* (Carroll and Baird, 1968) and *Pantylus*, there is an entepicondylar foramen about three-fifths of the way from the head to the distal end of the humerus, but the overall resemblance is closer to *Tuditanus*, in which the entepicondyle is more widely flared than the ectepicondyle. In *Pantylus* (Carroll, 1968, fig. 5), the capitellum lies on a prominently produced ectepicondyle, quite unlike the general tetrapod pattern. The distal and proximal planes of the humerus are twisted at almost a right angle to one another as in *Pantylus* (this feature is obscure in *Tuditanus*), but the shaft is somewhat more distinct. The articular ends are rugose, but there is no indication of immaturity; all the usual processes of the head are present, and the capitellum is a well-developed hemisphere. The humerus is 15 mm long, 6 mm wide across the head, slightly wider across the distal end, and has a minimum thickness of about 2 mm in the shaft.

Only the left radius is present; this has a semicircular head, narrow shaft —which is broken—and dilated distal end, much as in *Pantylus.* Only the right ulna is complete. It is 10 mm long, has a prominent olecranon, and is much narrower distally than proximally. There are closely associated but disarranged carpal elements and two metacarpals near the epipodials on the left side, but nothing can be confidently said of their original organization, nor of the number of digits.

The broken bones of the pelvic girdle overlap one another; while it is possible to recognize the individual elements, distinctive features cannot be discerned. The femur of the left side is complete, and the distal half of the right one is also present. The femur is gently sigmoidal, about 17 mm long, with a moderately developed adductor ridge and well-separated tibial condyles. The shaft has a diameter of about 2 mm in its narrowest portion; the distance across the distal condyles is 7.3 mm. A proximal fragment of an epipodial is present, but there is nothing more distal. The nature of the remains and the matrix demands "blind" removal of most of the blocks at the quarry, and in this process the holotype was truncated just behind the pelvis, probably separated from the referred specimen as mentioned earlier.

Imbricated scales may be seen alongside almost all the skeletal elements. Their fragility makes them extremely difficult to remove and prepare satisfactorily, but it has been possible to study the surface details of a number of them. They resemble very closely those of Pennsylvanian microsaurs illustrated by Carroll and Baird (1968, fig. 20). They are oblong, have a ridge along one border, and have radiate striae. The striae are especially well displayed on some of the scales of the referred specimen. A scale taken from the region of vertebra 17 of the holotype is about 1 mm wide by 3 mm long.

It is possible that other parts already collected from Interval 300 will eventually prove to be referable to *Trihecaton howardinus.* A specimen that consists mostly of finely denticulate palatal elements but also includes a partial maxilla with small, conical teeth (UCLA VP 1698) was identified in my earlier paper as a labyrinthodont amphibian, because of the infolded enamel (Vaughn, 1969). It may be of *T. howardinus*, but the specimen does not include the characteristic scales that would make this clear. Further excavation at Interval 300 is planned, and hopefully, better cranial materials may soon be found.

Discussion: Trihecaton must be regarded as a microsaur. Among Paleozoic tetrapods, the kind of first vertebra seen in *T. howardinus* is found only among the lepospondyl amphibians; and the combination of pleurocentral-intercentral construction of the vertebrae, well-developed limbs, and characteristically microsaurian scales—plus the fact that the neural arches are not, with the exception of the first vertebra, divided dorsally—rules out all lepospondyls but microsaurs. It is also clear that *Trihecaton* differs greatly from all previously described microsaurs. No others have infolded enamel (Carroll and Baird, 1968), although the bases of the teeth in *Trachystegos* do show a coarse fluting (Carroll, 1966). Although haemal arches have been found in several microsaurs including *Pantylus* (Carroll, 1968; Carroll and Baird, 1968), and small presacral intercentra have been reported in *Microbrachis* (Brough and Brough, 1967), none of the known microsaurs approaches *Trihecaton* in its large presacral intercentra with capitular facets for the ribs; and it must be remembered that *Trihecaton* also has well-developed haemal arches. The recently described lepospondyl *Acherontiscus* (Carroll, 1969) does have large intercentra, but the vertebral construction is so similar to that of the embolomerous labyrinthodonts that Carroll hesitated to assign *Acherontiscus* to any recognized order. The enamel in *Acherontiscus* is not infolded. It is difficult to escape the impression that *Trihecaton* is very primitive, despite its occurrence fairly high within the stratigraphic range of known microsaurs.

Two groups usually included in the Microsauria, the Adelogyrinidae and the Lysorophidae, are now considered by Carroll and Baird (1968) to be somewhat separate stocks; this is also the view of Thomson and Bossy (1970), who distinguish these two families from what they call "eumicrosaurs," a convenient term for present purposes. There does seem, however, to be general agreement that the adelogyrinids, lysorophids and eumicrosaurs are much more closely related to one another than any of these are to the remaining lepospondyls of traditional classification, the Nectridea and Aistopoda. Thomson and Bossy are of the opinion that the trend toward a holospondylous vertebral condition seen among the lepospondyls is not a reliable indicator of relationship but is, instead, a parallel tendency somehow correlated with small size. They conclude that the "Lepospondyli" are not a natural assemblage and suggest that the term be abandoned; with this I heartily concur.

Trihecaton would seem to be allied with the eumicrosaurs. The lysorophids are so different that they need hardly be considered, and no evidence of pleurocentral-intercentral construction of adelogyrinid vertebrae has ever been presented. Nevertheless, *Trihecaton* may represent something of a bridge between adelogyrinids and eumicrosaurs. Thomson and Bossy point out that the adelogyrinid jaw system was probably of the kinetic-inertial kind (see Olson, 1961), whereas the small coronoid process and other cranial features in the eumicrosaurs indicate a predominantly static-pressure system. *Trihecaton* has a prominent coronoid process. It is unfortunate that more of the skull is not known in *Trihecaton*, but in this seemingly annectent feature we may have reason to regard this genus as primitive.

It is certainly unwise to assume that all amphibians were derived from the Late Devonian ichthyostegalians—the variety of Mississippian forms is too great—but perhaps we may assume, in conservative style and for the time being, that the microsaurs and the labyrinthodont amphibians did have a common origin. If we do, we may perhaps regard the infolded enamel and the large intercentra in *Trihecaton* as additional marks of primitiveness. This suggestion invites dispute. Thomson and Bossy (1970) give reason to believe that such characters of tooth and vertebral structure may not be the reliable indices to relationship that they were once thought to be. However, their argument that infolding of the enamel is merely a function of large tooth size is considerably weakened by the occurrence of this character in such a small form as *Trihecaton*, even granted that the infolding is shallow. With regard to the vertebrae, Thomson and Bossy agree with Panchen (1967) that the structure of the centrum is extremely plastic. Differential composition of the centrum–multipartite versus unitary, differential emphasis on the parts when multipartite—may merely reflect different responses to problems of support and locomotion. Carroll (1969) regards the "embolomerous" construction of the vertebrae in *Acherontiscus* as probably associated with lengthening of the segments to assist in sinuous swimming movements. As Thomson and Bossy say (1970:14), "the combined centrum (divided or whole) is homologous in all amphibians," that is, not too much stress should be laid on the pleurocentrum and intercentrum in terms of strict homology. Despite these cautions, it does still seem that a combination of features in *Trihecaton*—infolding of the enamel, large presacral intercentra, prominent coronoid process—give this genus an overall aspect of primitiveness.

Trihecaton, at a Stephanian horizon, is of course too late in time to be considered as an actual "urmicrosaur." Adelogyrinids are known from the Lower Carboniferous (see Carroll, 1967); the problematic *Acherontiscus*, with a skull similar to that of eumicrosaurs, probably occurs in the lowest Upper Carboniferous (Carroll, 1969); and eumicrosaurs are known as low as the Westphalian B level, in the Joggins Formation of Nova Scotia (Carroll, 1966). Perhaps we may regard *Trihecaton* as a relict.

Of the eumicrosaurs, Carroll and Baird (1968) tentatively recognize the families Gymarthridae, Tuditanidae, Hyloplesionidae and Microbrachidae; and Carroll (1968) suggests that we consider the pantylids as a separate family. It is difficult to select from among these the family closest to the Trihecatontidae. For example, *Trihecaton* resembles the microbrachids in having a large number of presacral vertebrae (38-40 in *Microbrachis*) and in the presence of presacral intercentra (see Brough and Brough, 1967); but in its well-developed limbs and in the presence of an entepicondylar foramen in the humerus, *Trihecaton* resembles the shorter-trunked tuditanids (29 presacrals in *Tuditanus*) and pantylids (24 presacrals in *Pantylus*), with the resemblance to *Pantylus* extending to details of the pectoral girdle (see Carroll and Baird, 1968; Carroll, 1968). Aside, it may be noted that a long trunk in microsaurs is usually thought to be a sign of aquatic habits, and the feeble limbs in *Microbrachis* do seem to corroborate this, but *Trihecaton* has fairly sturdy limbs. Because of the incomplete nature of most microsaurian remains, there is at present little ground for decision as to whether an elongate column is primitive or advanced in this group. It may be of functional significance that the two microsaurs known to have presacral intercentra, *Trihecaton* and *Microbrachis*, also have long trunks. Perhaps the larger intercentra in *Trihecaton* are correlated with the sturdier limbs; Parrington (1967) has shown how the large intercentra in rhachitomous labyrinthodonts helped strengthen the column in terrestrial locomotion while still allowing flexibility, but rhachitomes are short-trunked. The alternation in shape of the neural spines may at first glance seem to be a special resemblance to *Pantylus* (see Carroll, 1968), but this phenomenon was apparently of widespread occurrence among late Paleozoic tetrapods and may be seen also in the Pennsylvanian lysorophid *Molgophis* (Dr. Donald Baird, personal communication, 1971) and even in the Early Permian reptile *Captorhinus* (Vaughn, 1970). *Trihecaton* stands alone among known microsaurs in its infolded enamel and its large presacral intercentra with capitular facets. It seems best, for now, not to pursue the placement of the Trihecatontidae within the Microsauria, but to leave this for later studies against, hopefully, a larger background of known forms.

Present knowledge of *Trihecaton* does not help solve the question of possible affinities of the microsaurs and the captorhinomorph reptiles. Romer (1969), in a recent and thorough study of the cranial anatomy of the Early Permian *Pantylus,* has demonstrated that the braincase and branchial arches of this form have a definitely amphibian cast, and comes to the conclusion that microsaurs and captorhinomorphs cannot have any antecedent-descendent relationship. Nevertheless, distinctions between microsaurs and captorhinomorphs continue to disappear; for examples, Carroll and Baird (1968) have demonstrated that the microsaurian first vertebra is a compound of elements probably homologous to the reptilian atlas and axis, and knowledge of *Trihecaton* adds to the growing list of microsaurs that have pleurocentral-intercentral vertebrae. Possibly this points to some remote community of origin of captorhinomorphs and microsaurs, but this is far from clear.

NEW INFORMATION ON *Desmatodon hesperis*

The genus *Desmatodon* was based by Case (1908) on *Desmatodon hollandi,* the holotype of which is a fragment of maxilla with four complete teeth and the root of a fifth (CM 1938, Carnegie Museum, Pittsburgh); the holotype was collected from the Round Knob Formation, Conemaugh Group, western Pennsylvania. I have named the species *Desmatodon hesperis* on the basis of a complete left maxilla with twelve teeth (UCLA VP 1706) taken from the Interval 300 quarry, and to this species I have already referred other materials: more teeth including "incisors," vertebrae, a humerus, and other elements (Vaughn, 1969). I have also pointed out that, while *D. hesperis* and *D. hollandi* are essentially similar as far as comparisons can be made, the tendency toward more conical shape of the teeth in *D. hesperis* gives this species a somewhat more primitive aspect. More materials referable to *D. hesperis* are now on hand from Interval 300, and these provide welcome additional information on the nature of *Desmatodon*, the only known Pennsylvanian member of that odd group of primitive reptiles—or seymouriamorph labyrinthodonts—called the diadectids.

UCLA VP 1745 (Fig. 4, A-C) consists of a braincase and firmly joined fragments of the posterior elements of the dermal skull roof. It was found on a plane that yielded various closely associated parts referable to *Desmatodon hesperis*, including teeth and vertebrae, but even without this association the diadectid nature of the specimen would be immediately obvious. It resembles in almost all ways the corresponding portion of the skull in the Early Permian *Diadectes*, and it may be safely assumed that the specimen is of *Desmatodon hesperis*. It has been distorted in such a way that the angle between the occipital surface and the dermal roof has been decreased, and parts of the braincase on the left side have been moved forward to leave a large gap between the ventral portions of the proötic and opisthotic. This distortion makes it difficult to take accurate measurements, but the original distance between the facets for the quadrate bones may be estimated at about 43 mm, and the distance between the lateralmost points of the paroccipital processes was about 48 mm. The specimen is very probably of an immature individual, to judge from the almost complete lack of ossification in the region of the otic labyrinth and by its close association with the juvenile maxilla described below. Because of the essential resemblance to *Diadectes*, for which excellent illustrations are available (Olson, 1947, 1966; Watson, 1954), description may be limited to salient features.

As in *Diadectes,* the opisthotic, supraoccipital, postparietal and tabular bones are indistinguishably fused; but the exoccipitals are separate, and the line of junction between the proötic and opisthotic can be easily discerned on either side. It is impossible to trace the suture between the parietal and postparietal bones with any confidence although it does seem clear that, again as in *Diadectes*, the postparietal has both occipital and roofing components. A symmetrically curved line across the postparietal area separates the rugose surface of the roof from the smoother occipital surface. A median ridge running ventrad from the postparietal, and a transverse ridge across the supraoccipital region mark out areas for attachment of occipital muscles. The parietal foramen is enormous, with almost the same diameter as the foramen magnum (about 12 mm), although distortion in both regions makes this only a rough comparison; the proportions in *Diadectes* are similar. The suture between the parietals can be followed for a short distance behind the foramen. About 1.5 cm to the left of the parietal foramen there is a deep longitudinal groove on the dorsal surface; this is seen also in certain *Diadectes* specimens (Watson, 1954, fig. 22), in which the groove partially demarcates the lateral parietal lappet from the main body of the parietal. A faint suture can be traced along the floor of the posterior part of this groove; this supports

Olson's (1950) arguments that an intertemporal bone was present in diadectids and that the parietal lappet is formed by this element. The nature of the groove, showing incomplete ossification between two dermal elements, is in accord with the pattern in *Diadectes*, of which Olson (1950:63) says, "Fusion of adjacent elements in the occipital and temporal regions appears to have been initiated at an early stage and to have progressed from the inner to the outer surface of the skull"; and it is also additional evidence of the immaturity of the specimen. Fractures and displacements in the region of the supratemporal make it impossible to delimit this bone satisfactorily, but an undulating longitudinal furrow probably marks its contact with the tabular.

One of the most interesting features of the specimen is the presence, on either side, of a fenestra between the postparietal and tabular regions. The thin, finished borders leave no doubt that these openings actually existed. The bone along the lateral border of the right fenestra is lacking, but the left fenestra is completely bounded. It is about 14 mm long; toward its posterior end it is about 8 mm wide as preserved but was probably narrower in life—the fragment of the tabular in this region is displaced slightly to the left, overriding the most posterior part of the facet for the supratemporal. *Desmatodon hesperis* is not really different from *Diadectes* in this feature. Although the fenestrae are rarely seen in *Diadectes,* they do occur in certain specimens (Case, 1911; Huene, 1913). Olson (1947) has commented on these openings in *Diadectes* and has pointed out that they do not lie in the position of "normal" reptilian temporal fenestrae. In view of the sporadic appearance of the fenestrae in *Diadectes*, and the indications that UCLA VP 1745 is immature, it certainly would be unwise to consider the fenestrae as diagnostic of *Desmatodon hesperis*, let alone the genus.

As in *Diadectes*, the supraoccipital sends a process under the postparietal, terminating abruptly at a line that corresponds to the separation dorsally between the roof and occipital surfaces. Despite the distortion that has driven the left proötic forward, both proötics are well preserved and resemble the same elements in *Diadectes*, extending upward and backward to their broad junctions with the opisthotics. The foramina for the abducent nerves penetrate the dorsum sellae, and a deep incisure that is more evident on the anterior margin of the right proötic presumably marks the place of exit of the trigeminal nerve. Jutting forward from just above the dorsum sellae are bilaterally placed plates that must represent the pilae antoticae; it is not clear that their lack of actual connection with the dorsum sellae might not be due to fracture and slight displacement, but they do seem to be separate elements, and perhaps this is another sign of immaturity. Olson (1966) has illustrated broad pleurosphenoids in this region in *Diadectes*, coösified with the dorsum sellae. Above and partly behind the upper end of the proötic, there is on the lateral surface of each opisthotic a deeply concave, elongate facet; this is the socket for the quadrate bone. This unusual mode of articulation of quadrate and braincase is known also in *Diadectes.* This specimen helps show that Olson (1966) has correctly interpreted the socket as occurring on the opisthotic in *Diadectes,* not on the proötic as was stated by Watson (1954).

The parasphenoidal rostrum is incomplete, but enough is left to show that it flared dorsad in front of the sella turcica. Only the left basipterygoid process of the basisphenoid is preserved. This has smooth anterodorsal and

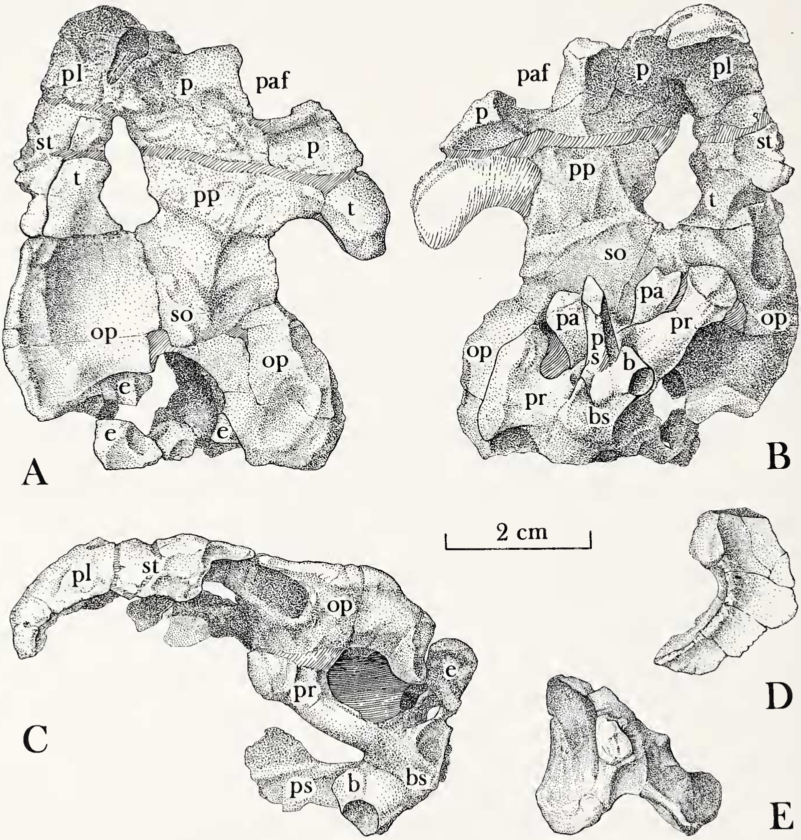

FIGURE 4. *Desmatodon hesperis:* A, dorsal, B, ventral, and C, left lateral views of braincase and connected dermal roofing elements (UCLA VP 1745); D, upper part of a right quadrate (UCLA VP 1746) in posterolateral view; E, lower part of another, larger right quadrate (UCLA VP 1747) in posterior view. Abbreviations: b, basipterygoid process; bs, basisphenoid; e, exoccipital; op, opisthotic; p, parietal; pa, pila antotica; paf, parietal foramen; pl, parietal lappet (=intertemporal?); pp, postparietal; pr, proötic; ps, parasphenoid; st, supratemporal; t, tabular. Because of fusion in the temporal region, some of the abbreviations mark general areas rather than distinctly demarcated elements. Line shading indicates matrix. Size indicated by the 2 cm scale.

anteroventral articular surfaces that are directed anteriorly and laterally. It is obvious that the joint between braincase and palate was mobile, unlike the condition in *Diadectes* where, despite an illustration by Watson (1954, fig. 18) that may give the opposite impression, the basisphenoid and pterygoid were firmly joined (see Olson, 1947). This feature could be interpreted as a mark of primitiveness of *Desmatodon hesperis*, but it could also be argued that it is merely another sign of immaturity of the specimen.

An upper part of a right quadrate bone (UCLA VP 1746, Fig. 4, D) was found near the braincase, to which it is appropriate in size. It has a well-defined condyle for articulation with the facet on the opisthotic bone. A lower part of another right quadrate (UCLA VP 1747, Fig. 4, E) found elsewhere in the quarry is obviously of a more mature individual, with a width of 25 mm across the articular end. The articular surface is divided into medial and lateral facets by a deep notch, and there is a large, rugose tubercle on the posterior surface above the notch, indicating a stapedial apparatus similar to that in *Diadectes* (see Olson, 1966). The resemblance of these specimens to *Diadectes* is very close (see Watson, 1954, fig. 24), and there can be little doubt that they are of *Desmatodon hesperis*.

A toothed right maxillary bone (UCLA VP 1748, Fig. 5, A, B) was found only a few inches away from the above-described braincase. The transversely widened, cusped teeth show that this specimen is of a diadectid, surely *Desmatodon hesperis*. The thin anteriormost part, where it overlapped the premaxilla, and the upper parts of the lateral wall have been broken away, but it is otherwise complete. Except for size and for certain features of the teeth, it is so similar to the holotypic maxilla that the description of the latter (Vaughn, 1969) suffices for both. A small projection on the medial side behind the last tooth is similar to one in the same position on the holotype, making it clear that the specimen is complete posteriorly and that no teeth have been lost. The new maxilla is 53 mm long as preserved, considerably shorter than the 77 mm long holotypic maxilla, and it is apparent that it is of a juvenile individual.

Whereas there are twelve teeth in the holotypic maxilla (Fig. 5, C), the juvenile maxilla has only eight, which seem to correspond to the first eight of the holotype. This correspondence is evident not only from the positions of the teeth with respect to the anterior end of the maxilla, but also from the fact that a narrow channel crossing the thickened medial surface of the maxilla ends ventrally at the plane between the third and fourth teeth in both specimens. Furthermore, the total length of the dental row in the juvenile is only slightly less than the length occupied by the first eight teeth of the holotype, 42 mm and 47 mm respectively. The juvenile teeth are all much shorter from front to back than the corresponding teeth of the holotype—for tooth 7 the respective dimensions are 2.6 mm and 5.2 mm—but they are separated by much longer spaces. It is obvious that with growth, the teeth of *D. hesperis* came to be replaced by more robust ones, and it is almost as obvious that the dental lamina must have become extended backward. These are common phenomena that may be observed also in living lizards (Edmund, 1969), but the elongation of the lamina in *D. hesperis* is striking when it is remembered that the transition from the juvenile dentition to that represented in the holotype involved the addition of four teeth, one-third of what is presumably the adult dentition. This is in sharp contrast to what is seen in the Early Permian *Diadectes*. For example, an immature specimen of *Diadectes san-*

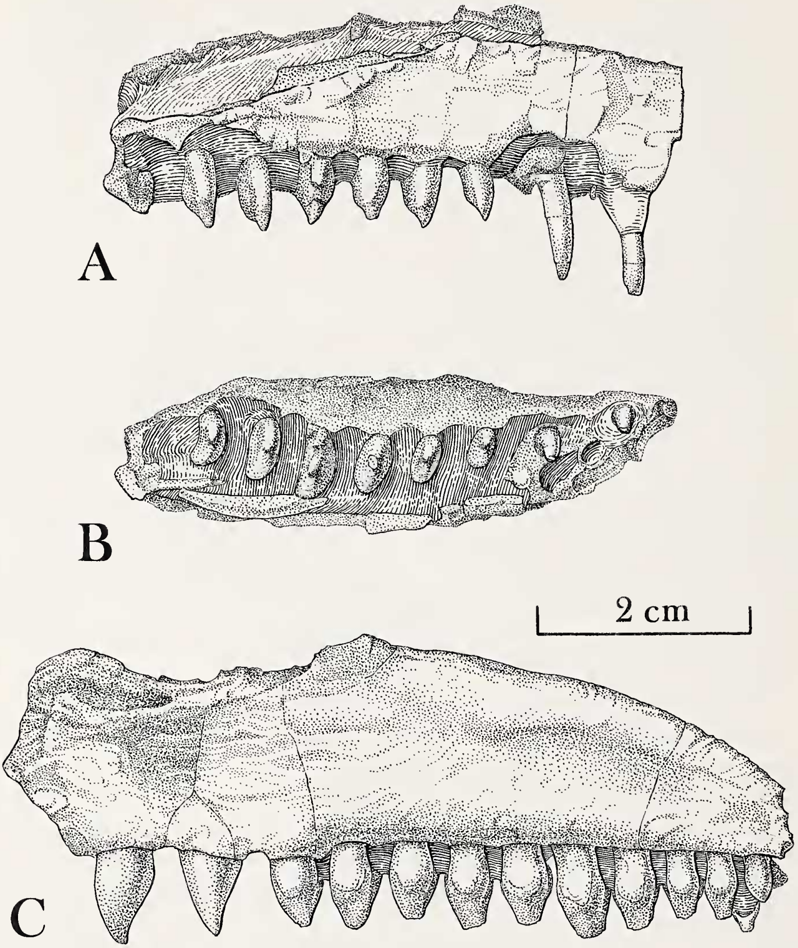

FIGURE 5. *Desmatodon hesperis:* A, lateral, and B, occlusal views of juvenile right maxilla (UCLA VP 1748); C, lateral view of holotypic left maxilla (UCLA VP 1706). Line shading indicates matrix and, in A and B, epoxy resin used to repair the specimen. Size indicated by the 2 cm scale.

miguelensis has a total of eleven teeth and empty alveoli in a maxilla only about 42 mm long (Lewis and Vaughn, 1965), and the number of maxillary teeth is hardly greater in adults of the various species of *Diadectes*, ranging from eleven to thirteen with eleven the usual number, as far as I have been able to determine from specimens and the literature. A specimen of *Diadectes lentus* at hand has a total of eleven teeth in a maxilla about 68 mm long. It is interesting to note that Romer (1952) has described a battery of eight small, diadectid-like cheek teeth contained in a length of only 11 mm, from the Conemaugh Group, and that Langston (1963) has described six diadectid-like teeth in a length of 10.5 mm, from the Lower Permian of Prince Edward Island; these specimens are, however, very poorly preserved, and their significance is difficult to assess.

Another notable contrast between the juvenile and holotypic dentitions is the much greater relative length of the first two teeth in the juvenile. In the holotype, the first two teeth are somewhat more acuminate than the succeeding, and they jut out slightly beyond the general tooth row. The difference is greatly accentuated in the juvenile, where the first two teeth are markedly incisiform, bowed with concave lingual sides, and twice as long as the succeeding teeth; the first and second teeth are each about 10 mm long, but the third is only about 5 mm long. It must be noted that the base of tooth 1 was lost during removal of the juvenile maxilla from the matrix, but this part was cast in epoxy resin from the impression, and the restored length is quite accurate. The teeth in the juvenile are, as might be expected, narrower from side to side than the corresponding teeth of the holotype—for tooth 7 the respective dimensions are 6 mm and 7.8 mm—but their lesser anteroposterior length makes them more bladelike. Labial, central and lingual cusps are present on teeth 5-8, but the lingual cusp is indistinct on teeth 3 and 4; all three cusps are distinct on teeth 3-8 of the holotype (actually, for the labial "cusp" the word "shoulder" would be more appropriate, this structure not being as well set off as in *Diadectes*). There are no signs of attrition on any of the teeth in the juvenile; this is remarkably different from the holotype, in which there are distinct wear facets on most of the teeth.

A combination of ways in which the juvenile maxillary dentition differs from that of the adult, much greater relative length and more incisiform aspect of the first two teeth, smaller number of teeth, teeth more bladelike and separated by longer spaces, lack of wear facets, fosters the suspicion that the change from juvenile to adult may have included a shift in dietary habit. *Diadectes* has been variously interpreted as herbivorous or molluscivorous; small pelecypods frequently found in association would seem to support the latter view, and it seems significant that small pelecypods are also known alongside the remains of *Desmatodon hesperis* in the Interval 300 quarry. It is hard to guess as to the diet of young *D. hesperis.* It is, of course, conceivable that the lack of wear facets on the juvenile teeth could be a result of more rapid replacement—it is known in crocodilians, for example, that the replacement rhythm becomes slower with age (Edmund, 1969)—but this would not account for the other juvenile-adult differences. Whatever further indications of a dietary shift may appear, it is at least clear that the transition from juvenile to adult in *Desmatodon hesperis* included much more pronounced dental changes than in *Diadectes*; in the immature specimen of *Diadectes sanmiguelensis* previously mentioned there is no great disparity between the first two maxillary teeth and those that follow.

Despite the above differences, the actual replacement of individual teeth in *Desmatodon hesperis* seems to have occurred in essentially the same manner as in *Diadectes* (see Edmund, 1960). A lingual pit was developed alongside each tooth, the base of the tooth became eroded, and the replacing tooth must have been ready for use soon after the overlying older tooth was shed, as shown by the lack of empty alveoli in both the juvenile and holotypic maxillae. Nevertheless, it will be shown that the cycle of tooth replacement in *Desmatodon hesperis* was different from what is known in *Diadectes.*

A diagrammatic analysis of the tooth-replacement cycle in *Desmatodon hesperis*, as inferred from the teeth of the holotypic maxilla, is presented in Figure 6. On the basis of intactness or attrition of the crown, and the degree of development of the lingual pit, five stages are arbitrarily delimited: newly erupted, not yet ankylosed (tooth 2); unworn but ankylosed (teeth 10, 12); worn, small lingual pit (teeth 1, 3, 5, 7); worn, large lingual pit (tooth 9); worn, base eroded (teeth 4, 6, 8, 11). If we assume that a "gap" exists between teeth 2 and 3, it will be seen that the teeth

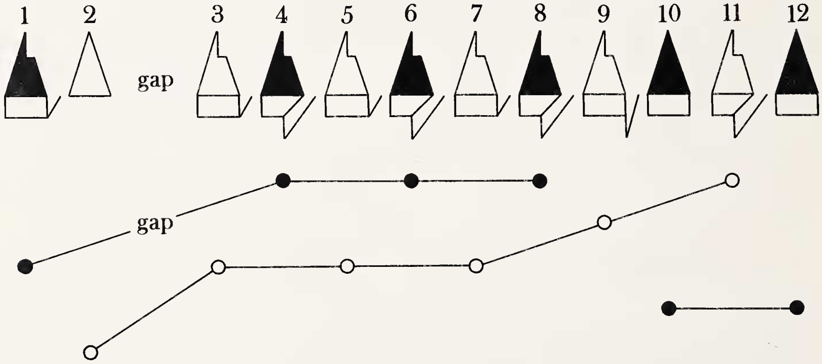

FIGURE 6. Analysis of tooth-replacement cycle based on the holotypic maxilla of *Desmatodon hesperis* (UCLA VP 1706). Filled-in and open symbols represent members of the two alternating replacement series. The symbols also indicate presence or absence of wear facets and the condition of the base, as: tooth 2, newly erupted, not yet ankylosed; tooth 10, unworn but ankylosed; tooth 1, worn, small lingual pit; tooth 9, worn, large lingual pit; tooth 4, worn, base eroded. The graph represents the partial waves of replacement, with the lowest level corresponding to newly erupted, not yet ankylosed, and the highest level corresponding to worn, base eroded.

can be arranged into two alternating replacement series, 1-gap-4-6-8-10-12 and 2-3-5-7-9-11, and it will also be seen that the cephalad waves of replacement overlap one another in an orderly manner, in accord with the usual tetrapod pattern (see Edmund, 1960). In the graphic representation of the waves, the five levels from lowest to highest correspond to the arbitrarily delimited stages described above, in the same order. Only if we assume the existence of the gap can the teeth be brought into such a pattern and, indeed, there is evidence for the reality of this gap, as will be brought out below. It is evident that the waves of replacement were long. Through graphic analysis in "Edmundian" style, it can be shown that a complete replacement wave included about seventeen teeth, from initial erosion of the old tooth to destruction and loss of the new, from birth to death of a tooth so to speak. This is considerably longer than replacement waves that have been analyzed in *Diadectes*, where a complete wave apparently included only about seven teeth (Edmund, 1960). The difference seems all the more profound when it is appreciated that a complete replacement wave can be seen within a jaw containing fourteen teeth in *Diadectes*, whereas it would take a jaw of at least thirty-three teeth to show a complete wave in *Desmatodon hesperis*.

Because of damage suffered by the juvenile maxilla when it was discovered through splitting of the enclosing matrix, most of the lingual pits cannot be studied, but those alongside the first two teeth are plainly evident, and these show that the second tooth has undergone some posteriorward displacement; this is also indicated by fragmentation of the bone at the base of the tooth. Thus it seems that there was originally an appreciable gap between the second and third teeth. In the holotypic maxilla there are short diastemata between the first and second and the second and third teeth, in marked contrast to the close packing in the rest of the row. However, a remnant of the base of an older tooth at the second position shows that the present tooth, newly erupted, and not yet ankylosed, must have moved posteriorward as it came in, creating the diastema between itself and the first tooth and reducing the gap between itself and the third. It is difficult to say whether or not this gap, which "shows up" in the replacement pattern as outlined above, was a constant feature in *Desmatodon hesperis*, but the condition is reminiscent of that noted by Edmund (1969:134) in certain of the teiid lizards where "Segments of the dentition may show regular rhythms, but these are not continuous along the entire jaw. The explanation may lie in the suppression of one or two adjacent tooth matrices to accommodate a single larger tooth." In the holotypic maxilla of *Desmatodon hesperis*, the disruption of regularity seems to be associated with development of the two short diastemata.

The fragmentary holotypic maxilla of *Desmatodon hollandi* has only four complete teeth and the root of a fifth; the represented stages are, from anterior to posterior: unworn but ankylosed; worn, base eroded; worn, small lingual pit; unworn but ankylosed; ?, large lingual pit. There are, of course, too few teeth to permit a definite statement, but it would seem that the replacement wave in *D. hollandi* was much shorter, and thus nearer to the condition in *Diadectes*, than in *D. hesperis*. As indicated in the initial description of *D. hesperis* (Vaughn, 1969), this species seems on other bases to be somewhat more primitive than *D. hollandi*, and it is conceivable that the longer replacement wave may present further grounds for differentiation, but nothing is known of the ranges of variation within the two species.

Even if it may eventually become necessary to set up a new genus based on *D. hesperis*, close relationship to *D. hollandi* would still be obvious; and the cranial parts described above should allay any doubts as to the diadectid affinities of *Desmatodon*. Although *Desmatodon* is more primitive in certain features than *Diadectes*, the two genera are nevertheless essentially similar; and it may be said definitely that the diadectid organization was well established in the Late Pennsylvanian. The known Early Permian diadectids form a closely knit group. Olson (1947) has summarized the various North American species, recognizing two genera, *Diadectes* and *Diasparactus*. *Phanerosaurus* and *Stephanospondylus* (probably synonyms) of the European Lower Permian are basically like *Diadectes* but, like *Desmatodon*, appear more primitive, having somewhat more acuminate teeth (Geinitz and Deichmüller, 1882, pl. 4) and, apparently, a mobile basipterygoid joint (Stappenbeck, 1905, fig. 4).

The phylogenetic origin of the diadectids remains obscure although *Tseajaia* from the Lower Permian of Utah does seem to provide a morphological link to seymouriamorph labyrinthodont amphibians (Vaughn, 1964). The recently described Late Mississippian anthracosaur *Mauchchunkia* may, as Hotton (1970) thinks, represent the ancestry of all "reptiliomorphs" including diadectids, but intermediate forms are still unknown. Romer (1964) has proposed that we consider *Diadectes* as a seymouriamorph rather than as a cotylosaur. This is consonant with the recent suggestion by Carroll (1970) that we exclude from definition as true reptiles all those forms that achieved reptilian morphological characteristics independently of the line that passed through romeriid captorhinomorphs; it would certainly be difficult to argue for romeriid-diadectid affinities. Perhaps we should follow the advice of Olson (1947) and think of diadectids as "parareptiles," but in an informal sense only, without intending the term as a taxonomic category.

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